

Evaluating the isotopic niche of beaked whales from the southwestern South Atlantic and Southern Oceans

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ABSTRACT: The study of species' niches is becoming increasingly important in ecological research with the growing need to understand how species and their habitat respond to rapid environmental changes. This kind of study is especially challenging in the case of oceanic and cryptic species such as beaked whales. We analyzed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in bone collagen to study interspecific variation in the isotopic niche of 8 species of beaked whales (*Berardius arnuxii*, *Hyperoodon planifrons*, *Mesoplodon bowdoini*, *M. grayi*, *M. hectori*, *M. layardii*, *Tasmacetus shepherdii* and *Ziphius cavirostris*) that stranded along the coast of Tierra del Fuego, Argentina, between 1967 and 2009. We found a spatial (e.g. feeding areas) and trophic (e.g. diet) isotopic segregation among these species, which are known to inhabit subantarctic to Antarctic waters. Isotopic analysis showed that, while spatial segregation seems to operate to a higher degree in species of the same genus (e.g. *Mesoplodon*), trophic differentiation allowed the co-existence of sympatric species from different genera (e.g. *Ziphius*, *Hyperoodon* and *Mesoplodon*). Our results agree with previous studies based on stomach content analyses. In addition to different trophic strategies, variation in habitat preferences were also revealed by stable isotope analysis. An isotopic trend in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values was found among beaked whales and possible prey species in accordance with previous information on other cetacean species known to have feeding areas in different ocean regions. The present study provides valuable ecological information about elusive and little-studied beaked whale species inhabiting the world's southernmost oceans.

KEY WORDS: Ziphiidae · $\delta^{13}\text{C}$ · $\delta^{15}\text{N}$ · Trophic niche · Subantarctic waters · Polar waters

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INTRODUCTION

The study of species' niches is becoming increasingly important in ecological research with the growing need to understand how species and their habitat respond to rapid environmental changes (Holt 2009, Wiens et al. 2009). The concept of 'ecological niche' took many different forms until a formal definition was proposed by Hutchinson (1957), who defined

niche as an n -dimensional space that encloses the complete range of environmental variables under which an organism (population or species) can live and replace itself indefinitely (Giller 1984, Holt 2009). In this sense, the study of a niche appears a complex and impossible task to accomplish. Thus, niches have been studied along just a few dimensions. A species' trophic niche, which is a subset of its ecological niche, plays a pivotal role in understand-

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ing how an animal community is structured, since it defines the way in which animals feed and use their habitat (Pianka 1974, Pusineri et al. 2008). Within biotic communities, the coexistence of closely related and ecologically similar species often requires some type of segregation between them (e.g. in trophic, spatial or temporal dimensions) as a way to reduce possible competition for resources (Pianka 1974, Whitehead et al. 2003, Pusineri et al. 2008). The strength of these interactions (e.g. competition) may vary in short- and long-time scales as a consequence of ecological and environmental variability. It also is known that the presence and abundance of top marine predators can be affected not only by the availability of their prey (bottom-up control) but also by environmental gradients, such as oceanic fronts or sea surface temperature (Cury et al. 2000, Renner et al. 2012). Studying the trophic niche of similar species within a community, therefore, is critical as an initial step towards understanding their ecological interactions. In addition, changes in these interactions may affect ecosystem processes in space and time, since top marine predators can also exert significant top-down controls via predation effects (Baum & Worm 2009, Reisinger et al. 2011).

An important cetacean community can be found ranging from the southwestern South Atlantic Ocean to Antarctica (Van Waerebeek et al. 2010). Especially the waters adjacent to Tierra del Fuego, the Falkland (Malvinas) Islands and Antarctica have been identified as key areas for beaked whales (MacLeod & Mitchell 2006). The highly variable oceanographic features and environmental conditions of these ocean regions provide suitable habitats for more than 25% of all beaked whale species and 50% of all beaked whale genera (Otley et al. 2012). Despite the efforts of long-term sighting and stranding programs carried out in this region (see Goodall et al. 2008, Santora & Brown 2010, Otley 2012, Otley et al. 2012, among others), beaked whales are still the least known group of marine mammals, due in part to their offshore and cryptic lifestyle. They are known to spend ~20% of their time foraging at mesopelagic depths (~1000 m depth), generally around islands and in upwelling areas, with dives lasting up to 1 h or longer when they hunt for deep-water squid and fish (MacLeod et al. 2006, Groom et al. 2014). Beaked whale species appear to overlap in their trophic niche, which may cause competition between species (MacLeod et al. 2003). However, differences between genera have been detected through conventional diet studies, mostly related to spatial (e.g. different foraging areas) and/or to trophic segregation

(e.g. prey taxa, size of the prey consumed) (reviewed in MacLeod et al. 2003).

Stable isotopes of carbon and nitrogen have been routinely used to provide valuable information about some aspects of an animals' trophic niche (e.g. diet, foraging habitat). Thus, the term 'isotopic niche' has been proposed as a way to approximate the trophic dimensions of a niche (Newsome et al. 2007). This approach relies on the principle that different foraging habits may produce distinctive isotope signals since the isotope composition of an animal's diet will be reflected in its tissues in a predictable manner (DeNiro & Epstein 1978, 1981, Minagawa & Wada 1984). Due to physiological processes, consumers are enriched in heavier isotopes (e.g. ^{13}C , ^{15}N) with respect to their diets; the resulting isotopic difference has been referred to as trophic discrimination (Newsome et al. 2010). However, the reflection of dietary isotopic values in a consumer's tissue may vary with diet quality, the tissue analyzed, the size of the animal, ontogenetic stage, nutritional status and many other factors (Ben David & Flaherty 2012, Phillips 2012). Despite these variations $\delta^{13}\text{C}$ values in a consumer's tissue can be used to identify different nutritional sources if all potential foods are isotopically discrete and provide information on the main primary producers in a trophic web (Michener & Kaufman 2007). Additionally, $\delta^{15}\text{N}$ values, which reflect nutritional sources, are also used as indicators of trophic positions (Post 2002). Thus, differences in isotope values among beaked whales can be used to assess trophic (diet) segregation. Further, isotopic values of primary producers (e.g. phytoplankton) in marine ecosystems also vary spatially (and temporally) in a complex manner, generating an isotopically heterogeneous seascape (Goericke & Fry 1994, Lara et al. 2010, Quillfeldt et al. 2010). Since isotopic baseline values (e.g. phytoplankton) can cascade up food webs, differences in isotopic values between beaked whales can also be linked to habitat segregation (e.g. distinct foraging areas) (Best & Schell 1996, Graham et al. 2010). In this manner, through the use of the isotopic niche concept, both isotopic axes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) can supply information about the bionomic (e.g. diet) and scenopoetic (e.g. habitat) components of a trophic niche (Newsome et al. 2007) of these mesopelagic marine consumers.

The ecological information gained using stable isotopes also offers a variable temporal window that depends on the tissue analyzed (Newsome et al. 2010). For oceanic cetaceans such as beaked whales, which are difficult to locate and observe during feeding activities, bone collagen is a suitable tissue for analysis to compare their general trophic habits and

foraging areas. In contrast to soft and active metabolic tissues, such as liver, plasma and muscle, bone collagen can be sampled from stranded animals since it is well-preserved. Additionally, due to its low isotopic turnover rate, it provides ecological information for many years (~5 to 10 yr) and can thus be used to assess long-term foraging habits (Koch 2007, Newsome et al. 2010).

Different quantitative tools have been used to characterize the isotopic niche of animals, including statistical procedures using ANOVA to compare sample means and isotopic variances (Bearhop et al. 2004), Euclidean methods such as convex hull (Layman et al. 2007) and Bayesian ellipses using SIBER (stable isotope Bayesian ellipses in R, Jackson et al. 2011). Using these approaches, it is possible to define the trophic diversity or specialization through the area occupied in a bivariate space (isotopic niche area) and evaluate resource partitioning through the extent of overlap in the isotopic niche area among species in a community (Jackson et al. 2012, Ryan et al. 2013, Browning et al. 2014).

With the objective of exploring possible niche partitioning between species of beaked whales, and paying special attention to trophic and spatial dimensions, carbon and nitrogen stable isotope composition in bone collagen was analyzed in specimens found stranded along the coasts of Tierra del Fuego since 1967 (Goodall et al. 2008). Also, isotopic data of other cetaceans inhabiting this vast area and that of possible prey were compared to establish an isotopic spectrum of the cetacean community and its prey, from the north and/or coastal habitat to southern and/or oceanic environments.

MATERIALS AND METHODS

Species and sample collection

Eight beaked whale species belonging to 5 genera (*Mesoplodon*, *Ziphius*, *Hyperoodon*, *Tasmacetus* and *Berardius*) were found stranded along the north-eastern and southern coast of Tierra del Fuego, Argentina (52–54° S and 68–69° W) between the years 1967 and 2009, as part of an ongoing, long-term study (Goodall et al. 2008). Samples of bone (n = 74) from the skull were taken from Arnoux's beaked whale (*B. arnuxii*, n = 1), southern bottlenose whale (*H. planifrons*, n = 11), Andrew's beaked whale (*M. bowdoini*, n = 1), Gray's beaked whale (*M. grayi*, n = 12), Hector's beaked whale (*M. hectori*, n = 2), Layard's beaked whale (*M. layardii*, n = 20), Shep-

herd's beaked whale (*T. shepherdii*, n = 4) and Cuvier's beaked whale (*Z. cavirostris*, n = 23). Specimens are held in the Goodall collection at the Acatushún Museum of Austral Marine Birds and Mammals, Harberton Ranch, Tierra del Fuego (for general information on each species, see Table S1 in the Supplement at www.int-res.com/articles/suppl/m581p183_supp.pdf).

Beaked whale isotope values were also compared with bone collagen isotope values from other cetacean species to establish an isotopic spectrum of the cetacean community from the coastal habitat adjacent to Tierra del Fuego (e.g. *Cephalorhynchus commersonii*, data from Riccialdelli et al. 2013) to southern and oceanic environments (e.g. *Lagenorhynchus cruciger*, *Phocoena dioptrica*, data from Riccialdelli et al. 2010, and *Eubalaena australis*, present study). Based on previously published dietary studies, isotope data of possible prey (e.g. fish, squids and crustaceans) were selected from the same environments mentioned above (data from Dunton 2001, Ciancio et al. 2008, Schmidt et al. 2004, Polito & Goebel 2010, Riccialdelli 2011, Raya Rey et al. 2012, Stowasser et al. 2012, Polito et al. 2013, Riccialdelli et al. 2013, Alvito et al. 2014, Zangrando et al. 2016). Also, a set of muscle samples of benthopelagic fish from polar waters adjacent to South Georgia, South Sandwich and South Orkney islands (~54° to ~61° S and ~26° to ~55° W) were collected during the LAMPOS (Latin America Polarstern Study) survey in April 2002 and then processed and analyzed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

Stable isotope analysis

Cetacean bone collagen was extracted by demineralization in 0.2 N HCl for ~72 h at room temperature with frequent replacement of fresh HCl solution during this period. Samples were rinsed with distilled water to achieve a more neutral pH. Lipids were removed by repeated rinsing with a 2:1 chloroform:methanol solution. The resulting collagen preparations were then rinsed several times with distilled water and dried in an oven at 60°C for ~48 h. Prey muscle samples were oven-dried at 60°C for 48 h, and lipids were extracted in the manner described before. Dried samples were weighed into tin capsules (3 × 5 mm) and analyzed with a Thermo DELTA V Advantage isotope-ratio mass spectrometer at the Instituto de Geocronología y Geología Isotópica (INGEIS), Buenos Aires, Argentina. Results are expressed in delta (δ) notation using the equation:

$$\delta = 1000 \frac{R_S - R_R}{R_R} \text{‰} \quad (1)$$

were $\delta = \delta^{13}\text{C}$ or $\delta^{15}\text{N}$; R_S and R_R are the $^{13}\text{C}:^{12}\text{C}$ or $^{15}\text{N}:^{14}\text{N}$ ratios of the sample and reference standard, respectively. The standards are Vienna Pee Dee Belemnite (VPDB) for carbon, and AIR (atmospheric N_2) for nitrogen (Gonfiantini 1978, Coplen et al. 1992). The units are expressed as ‰. Based on 3 internal standards (caffeine std, sugar std and collagen TRACE), the within-run standard deviation (SD) was 0.2‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Coplen et al. 2006). Since all beaked whale samples were collected from 1967 to 2009, we applied a correction factor of $-0.022 \text{‰ year}^{-1}$ to all carbon isotope sample values to account for the Suess effect (Francey et al. 1999, Idermühle et al. 1999). Atomic C:N ratios of bone collagen ($2.9 < \text{C:N} < 3.5$) and fish muscle (< 3.2) was in the expected range for pure protein-lipid extracted samples (Ambrose 1990, Post et al. 2007).

Statistical analysis and data treatment

A Kolmogorov-Smirnov test (K-S test) was used to test normality of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, and an F -test (Levene's test) was used to test homogeneity of variance within a species. Since the data did not meet the requirements for parametric statistical tests, differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among species were assessed using a nonparametric Kruskal-Wallis test (H -test), followed by Mann-Whitney (U -test) pairwise comparisons. Differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ variance among species were assessed with an F -test (Levene's test) as a way to evaluate trophic segregation/overlap among species. For all calculations, we tested significance at the $\alpha = 0.05$ level. *B. arnuxii*, *M. bowdoini* and *M. hectori* were not compared due to small sample size ($n \leq 2$); thus, we only provide descriptive comparisons.

As a way to complement statistical tests, a cluster analysis (average linkage method and Euclidean distance) was used, based on mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for each species, to identify spatial isotopic patterns and determine general trophic relationships among the beaked whale species analyzed.

Using the groups identified in the cluster analysis, we estimated trophic position (TP) for each cetacean species. The $\delta^{15}\text{N}$ values from each individual were used; thus, a mean TP and SD is provided for each species. TP was estimated using the equation proposed by Hobson & Welch (1992):

$$\text{TP}_{\text{cet}} = [(\delta^{15}\text{N}_{\text{cet}} - \delta^{15}\text{N}_{\text{baseline}}) / \text{TDF}] + \text{TP}_{\text{baseline}} \quad (2)$$

where the TP_{cet} is the TP of each species of cetacean considered, $\delta^{15}\text{N}_{\text{cet}}$ is the nitrogen isotope composition of the species of cetacean considered, $\delta^{15}\text{N}_{\text{baseline}}$ and $\text{TP}_{\text{baseline}}$ are the mean nitrogen isotope composition and the trophic position, respectively, of the baseline considered. Mean (\pm SD) $\delta^{15}\text{N}$ values of euphausiids (*Euphausia lucens* and *E. superba*) were used as a baseline of 3 general areas detected in the cluster to estimate trophic position: (1) mean $\delta^{15}\text{N}$ values ($7.3 \pm 0.8\text{‰}$) of euphausiids reported by Ciancio et al. (2008) were used as a baseline for sub-antarctic waters (SW) adjacent to Tierra del Fuego, (2) a mean $\delta^{15}\text{N}$ value of $4.3 (\pm 0.8\text{‰})$ was calculated based on $\delta^{15}\text{N}$ values of euphausiids reported by Schmidt et al. (2004) and Stowasser et al. (2012) for waters adjacent to South Georgia Island and the Scotian Sea and was used as baseline for Antarctic Circumpolar Current (ACC) waters, and (3) a mean $\delta^{15}\text{N}$ value of $3.3 (\pm 0.5\text{‰})$ was calculated based on $\delta^{15}\text{N}$ values for euphausiids, reported by Dunton (2001), Schmidt et al. (2004), Polito & Goebel (2010), Raya Rey et al. (2012) and Polito et al. (2013) from the South Shetland Islands and Antarctic Peninsula and was used as a baseline for polar waters (PW) near Antarctica. We assumed a trophic position of 2 for all euphausiids. The TDF is the trophic discrimination factor, estimated as the difference in $\delta^{15}\text{N}$ values between consumers and their prey. To estimate the TP_{cet} , we used a mean TDF of 3.4‰, which is used for a wide variety of animal taxa when experimental TDFs are unavailable as in our case (Minagawa & Wada 1984, Cabana & Rasmussen 1996, Post 2002). Data from possible prey were corrected for trophic and tissue discrimination to allow for direct comparison with cetacean bone collagen. For isotopic data from cephalopod beaks, we applied 2 corrections. The first one was used to approximate beak values to $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the mantle (soft tissue) based on isotope values reported by Hobson & Chérel (2006) under a controlled captive study. Based on these data, we calculated a mean isotopic difference of -0.1‰ and $+3.3\text{‰}$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively, between the lower beaks (excluding the rostral tip, since they represent the neonatal diet) and the mantle of the cuttlefish *Sepia officinalis*. Then, for all soft tissues (e.g. mantle for squids and muscle for fish), we applied a second general correction of $+5\text{‰}$ and $+3.4\text{‰}$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, respectively, for trophic and tissue discrimination, to allow for direct comparison with cetacean bone collagen (Howland et al. 2003, Hedges et al. 2005, Koch 2007). For prey bone collagen, we applied a general correction of $+1\text{‰}$ and $+3.4\text{‰}$ for trophic discrimination only

(DeNiro & Epstein 1978, 1981, Minagawa & Wada 1984, Hare et al. 1991, Hedges et al. 2005, Koch 2007).

To evaluate the isotopic niche and possible overlap between species, isotopic standard ellipse areas corrected for small sample size (SEAc) were calculated based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data. The SEAc fits 40% of the data and represents the mean core population isotopic niche exploited by a particular species (Jackson et al. 2011, 2012). The Bayesian estimate of SEA (SEA_B) was also calculated for statistical comparisons of the isotopic niche area between groups (Jackson et al. 2011). In addition, the overlap between ellipses were calculated by using the SEAc of each ellipse, expressed as the area in units of per mil squared ($\% ^2$). The SEAc, SEA_B and the isotopic niche overlap were calculated using SIBER (Jackson et al. 2011) or SIAR in R (Parnell et al. 2010, R Development Core Team 2012). The trophic diversity or specialization was estimated through the isotopic niche area (SEAc) occupied by each species. Whilst a small SEAc may indicate a narrow trophic diversity (or high resource specialization), a large one may indicate a wide trophic diversity for the entire population under analysis (which could be composed of a population of generalist or a population of specialists). A possible niche partitioning between species was estimated through the extent of overlap between ellipses. A substantial isotopic niche overlap indicates an overlap in resource utilization between species, which can potentially lead to interspecific competition pressure if resources become limited. A small isotopic niche overlap between species indicates a possible niche partitioning (Jackson et al. 2012).

In addition, Layman's metrics (Layman et al. 2007) were calculated to help the evaluation of trophic diversity and niche partitioning: the mean distance to centroid (CD) was used as a measure of trophic diversity of the population; the variation of $\delta^{15}\text{N}$ (Nr) was used as a measure of the ability to consume organisms occupying different trophic levels; the variation of $\delta^{13}\text{C}$ (Cr) was used as a measure of the diversity in the exploitation of basal resources; and the SD of the nearest neighbor distance (SDNND) was used as a measure of the distribution/dispersal of individuals within an isotopic space. In order to avoid possible influences on Layman's metrics by the isotopic variation in baselines between ocean regions (Hoenghaus & Zeug 2008), these measurements were only compared between those species considered to share the same general foraging area. Layman's metrics were calculated using also the SIBER package of SIAR in R.

RESULTS

Cetacean species

Mean isotopic bone collagen values in the 8 beaked whale species ranged from -19.9 to -14.3% for $\delta^{13}\text{C}$ and from 11.5 to 16.5% for $\delta^{15}\text{N}$. The most enriched ^{13}C and ^{15}N values were found in *Mesoplodon grayi* and *Tasmacetus shepherdi*, and the most depleted were found in *Berardius arnuxii* and *M. hectori* (Fig. 1, Table 1). Significant differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were found between the beaked whales ($H = 39.89$, $df = 4$, $p < 0.001$; $H = 30.05$, $df = 4$, $p < 0.001$, respectively; see Table 2 for pairwise comparisons). While there were no significant differences in $\delta^{13}\text{C}$ -associated variances (Levene's test, $p = 0.495$), there was a small difference in $\delta^{15}\text{N}$ -associated variances (Levene's test, $p = 0.041$).

Inshore and subantarctic cetacean species (*Cephalorhynchus commersonii*) had the highest values in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ among all studied cetaceans, whilst southern and cold-water predators (e.g. *Phocoena dioptrica*, *Lagenorhynchus cruciger* and *Eubalaena australis*) had the lowest values in both isotopes. Estimated TPs ranged between 3.1 for *E. australis* to 5.0 for *C. commersonii* (Table 1). All beaked whales fell between the 3rd and 4th trophic levels with significant differences between their TPs ($H = 31.00$, $df = 4$, $p < 0.001$; see Table 2 for pairwise comparisons).

Cluster analysis

Cluster analysis identified the main trophic relationships between the beaked whales based on their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Fig. 2). This analysis was separated by species enriched in ^{13}C and ^{15}N (e.g. *T. shepherdi*) from those with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values depleted in the heavier isotopes (e.g. *B. arnuxii*). The cluster identified 4 main beaked whale groups; we considered Groups 1 and 2 as subantarctic temperate-water species mainly found in SW—Group 1: *T. shepherdi*, *M. grayi*; and Group 2: *Ziphius cavirostris* and *M. bowdoini*; and Groups 3 and 4 as subantarctic and Antarctic cold-water species mainly found in PW—Group 3: *M. layardii*, *Hyperoodon planifrons*; and Group 4: *B. arnuxii*, *M. hectori*. As seen in Fig. 1, an area with different isotopic values between northern and southern groups can be detected, probably corresponding with the ACC.

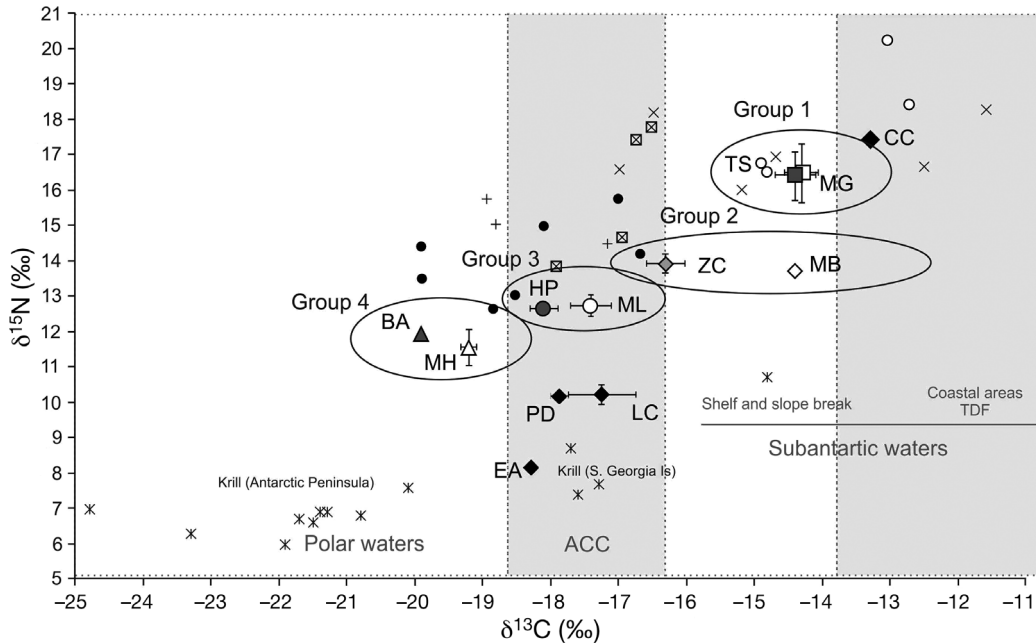


Fig. 1. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (\pm SE) of cetacean species and prey groups from the southwestern South Atlantic and Southern Oceans. Oval outlines indicate beaked whale groups that were detected by cluster analysis. Light gray and white areas indicate isotopic boundaries of main geographic foraging habitats based on the isotopic data of krill: subantarctic waters (coastal and shelf and slope break adjacent to Tierra del Fuego), Antarctic Circumpolar Current (ACC) and polar waters, as identified by Phillips et al. (2009) and Raya Rey et al. (2012) but with trophic correction applied. Cetacean species: TS = *Tasmacetus shepherdi*; MG = *Mesoplodon grayi*; ZC = *Ziphius cavirostris*; MB = *M. bowdoini*; ML = *M. layardii*; HP = *Hyperoodon planifrons*; MH = *M. hectori*; BA = *Berardius arnuxii*; CC = *Cephalorhynchus commersonii*; PD = *Phocoena dioptrica*; LC = *Lagenorhynchus australis* (CC, PD and LC; data from Riccialdelli et al. 2013); EA = *Eubalaena australis*. Prey groups: (O) subantarctic benthopelagic fish; (●) Antarctic benthopelagic fish; (×) SW neritic and oceanic squids (data from Alvito et al. 2015; Riccialdelli et al. 2013), (⊠) ACC squids (data from Alvito et al. 2015); (+) PW squids (data from Alvito et al. 2015); (*) Krill = *Euphausia superba* (data from Dunton 2001, Schmidt et al. 2004, Polito & Goebel 2010, Raya Rey et al. 2012, Stowasser et al. 2012, Polito et al. 2013), *E. lucens* (data from Ciancio et al. 2008). Prey data are shown with trophic and tissue correction factors incorporated

Prey species

Isotope data of possible prey followed the isotope values of the cetaceans after application of trophic and tissue-specific correction to allow for direct comparison (Fig. 1, Table 3). A clear stable isotope trend in prey species is observed, from subantarctic/sub-tropical and neritic species (e.g. *Illex argentinus*, *Loligo gahi*, *Macruronus magellanicus*, *Merluccius australis*) with the highest values in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, and oceanic and polar prey with the lowest values in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, such as the ice fish (e.g. *Champsocephalus aceratus*) and Antarctic squids (e.g. *Galioteuthis glacialis*). Isotope values of krill (*Euphausia lucens* and *E. superba*), as with the prey species mentioned above, were in accordance with the 3 southern areas identified, SW (i.e. isotopic data from specimens collected in southern Patagonia), ACC (i.e. isotopic data from specimens collected near South Georgia Islands) and PW (i.e. isotopic data from specimens collected near the Antarctic Peninsula).

Isotopic niche

The widest isotopic niche area (SEAc) was found in *M. layardii* and in *Z. cavirostris*, followed by *M. grayi* and *T. shepherdi*. *H. planifrons* occupied the smallest isotopic niche area (Fig. 3, Table 4). *T. shepherdi* had an isotopic niche overlap with *M. grayi* only, corresponding to 63 and 50% of their SEAc, respectively. *M. grayi* also showed overlap with *Z. cavirostris* with 15 and 11%, respectively, but no overlap with *H. planifrons* or *M. layardii*. Also, there was a high level of isotopic niche overlap between *Z. cavirostris* (43%) with *M. layardii* (41%). *H. planifrons* had an isotopic niche overlap with *M. layardii* corresponding to 80 and 20% of their SEAc, respectively (Fig. 3).

In relation to Layman's metrics, a cluster was detected among Group 1 and 2 species; the highest value in Cr was found in *Z. cavirostris* and in Nr in *M. grayi*. *T. shepherdi* showed a small range in both metrics, but high SDNND. The greatest CD in this

Table 1. Bone collagen stable isotope composition and trophic position estimated (TP) for 8 species of beaked whales and other cetacean species stranded along the coast of Tierra del Fuego, Argentina. Values of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and TP are means \pm SD; n = number of individuals analyzed. Foraging area identified through stable isotope analysis: SW = subantarctic waters, ACC = Antarctic Circumpolar Current, PW = polar waters

Cetacean family/ scientific name	Common name	n	$\delta^{13}\text{C}$ (‰)		$\delta^{15}\text{N}$ (‰)		C/N		TP		Foraging area	Source
			Mean	SD	Mean	SD	Mean	SD	Mean	SD		
Ziphiidae												
<i>Berardius armuxii</i>	Arnoux's beaked whale	1	-19.9		11.9	11.9	3.5		4.5		PW	Present study
<i>Hyperoodon planifrons</i>	Southern bottlenose whale	11	-18.1	0.7	12.6	0.7	3.4		4.7	0.2	PW	Present study
<i>Mesoplodon bowdoini</i>	Andrew's beaked whale	1	-14.4		13.7		3.3		3.9		SW	Present study
<i>Mesoplodon grayi</i>	Gray's beaked whale	12	-14.4	1.2	16.5	2.6	3.4		4.7	0.8	SW	Present study
<i>Mesoplodon hectori</i>	Hector's beaked whale	2	-19.2	0.3	11.5	0.8	3.5		4.4	0.2	PW	Present study
<i>Mesoplodon layardii</i>	Layard's beaked whale	20	-17.4	1.4	12.8	1.5	3.3		4.5	0.5	ACC	Present study
<i>Tasmacetus shepherdi</i>	Shepherd's beaked whale	4	-14.3	0.4	16.5	1.7	3.5		4.7	0.5	SW	Present study
<i>Ziphius cavirostris</i>	Cuvier's beaked whale	23	-16.3	1.3	13.9	1.4	3.4		3.9	0.4	SW	Present study
Delphinidae												
<i>Cephalorhynchus commersonii</i>	Commerson's dolphin	220	-13.3	1.2	17.4	1.0	2.9		5.0	0.3	SW	Riccialdelli et al. (2013)
<i>Lagenorhynchus cruciger</i>	Southern right whale dolphin	5	-17.2	1.0	10.2	0.8	2.8		3.7	0.2	ACC	Riccialdelli et al. (2010)
<i>Phocoena dioptrica</i>	Spectacled porpoise	87	-17.9	1.2	10.1	0.9	2.9		3.7	0.3	ACC	Riccialdelli et al. (2010)
Balaenidae												
<i>Eubalaena australis</i>	Southern right whale	1	-18.3		8.2		3.2		3.1		ACC	Present study

group was found in *M. grayi*, being similar in the other 2 species (Table 4). The metrics in Group 4 were not calculated, as was the case for *M. bowdoini*, from Group 2, due to insufficient sample size (≤ 2). Thus, only species in Group 3 were compared. *M. layardii* had a larger Cr and Nr, a higher CD and greater SDNND compared to *H. planifrons* (Table 4).

DISCUSSION

We found large variation in bone collagen $\delta^{13}\text{C}$ ($\sim 7.8\text{‰}$) and $\delta^{15}\text{N}$ ($\sim 9.0\text{‰}$) values among the 8 beaked whale species analyzed. This was also found in previous studies for small cetaceans inhabiting the subantarctic waters off Tierra del Fuego (Riccialdelli et al. 2010) and other adjacent regions, such as southern Brazil (Botta et al. 2012, Bisi et al. 2013). Along with this isotopic variation, a significant segregation in both mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values was evident among species. Interspecific isotopic differences may result from different prey choices, different foraging areas, and/or variation in isotopic baseline values through time (e.g. Quillfeldt et al. 2015). The bone collagen of beaked whales integrates several years of ecological information, but it is a tissue that cannot track short-term changes in baseline isotope values which may have resulted from variation in productivity, nutrient availability or temperature over a short period of time, due to its low isotopic turnover rate (Newsome et al. 2010). Thus, the isotope variation between species is expected to be a reflection of differences in their isotopic niche, which may be the result of distinctive diet and/or foraging habitat.

Spatial segregation: foraging areas

Despite the fact that all the cetaceans analyzed in this study were found stranded along coastal areas of Tierra del Fuego, ocean currents are known to transport dead or incapacitated animals from other areas where they commonly live (Groom et al. 2014). The 8 beaked whale species analyzed are known to inhabit areas from subantarctic towards polar waters (Bastida & Rodriguez 2009, Van Waerebeek et al. 2010), areas characterized by a great variation in oceanographic conditions and productivity (Acha et al. 2004, Glorioso et al. 2005).

Differences in isotope values between these oceanic regions may explain the isotopic differences found between beaked whales. Variations in baseline isotopic values (e.g. particulate organic matter [POM])

Table 2. *U*-test pairwise comparisons among bone collagen $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and trophic position estimated (TP) values of beaked whale species. Each column includes the results for the *U*-tests. Significant *p*-values ($p < 0.05$) are indicated in **bold**

Pairwise comparison	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	TP
<i>Tasmacetus shepherdii</i> versus <i>Mesoplodon grayi</i>	0.865	0.762	0.762
<i>Tasmacetus shepherdii</i> versus <i>Ziphius cavirostris</i>	0.011	0.019	0.019
<i>Tasmacetus shepherdii</i> versus <i>Hyperoodon planifrons</i>	0.005	0.005	0.948
<i>Tasmacetus shepherdii</i> versus <i>Mesoplodon layardii</i>	0.006	0.008	0.462
<i>Mesoplodon grayi</i> versus <i>Ziphius cavirostris</i>	0.001	0.004	0.004
<i>Mesoplodon grayi</i> versus <i>Hyperoodon planifrons</i>	0.000	0.004	0.926
<i>Mesoplodon grayi</i> versus <i>Mesoplodon layardii</i>	0.000	0.002	0.090
<i>Ziphius cavirostris</i> versus <i>Hyperoodon planifrons</i>	0.000	0.001	0.000
<i>Ziphius cavirostris</i> versus <i>Mesoplodon layardii</i>	0.002	0.000	0.000
<i>Hyperoodon planifrons</i> versus <i>Mesoplodon layardii</i>	0.060	0.549	0.001

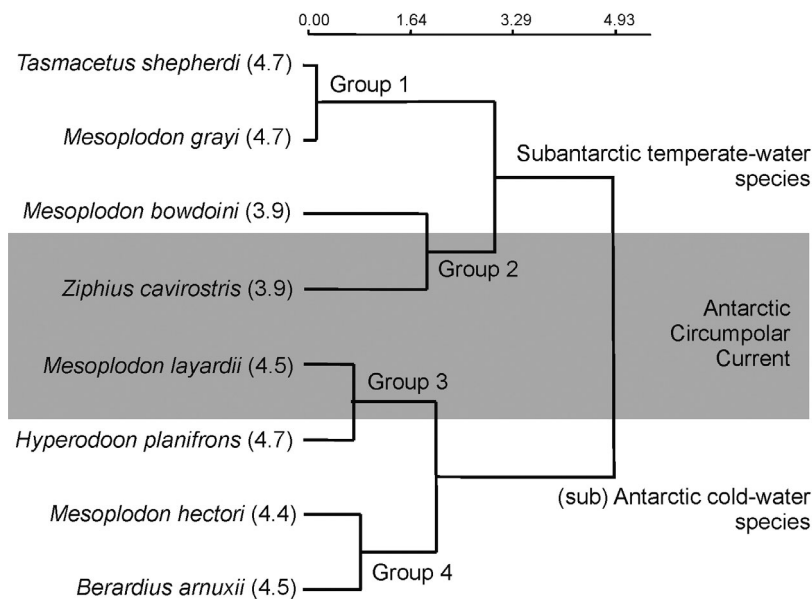


Fig. 2. Cluster analysis (average linkage method and Euclidean distance) for 8 species of beaked whales based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. The x-axis represents the distance metric (Euclidean). Groups 1 and 2 were considered to be subantarctic temperate-water species and Group 3 and 4 (sub) Antarctic cold-water species. An area with different isotopic values between northern and southern groups can be detected, likely related to the Antarctic Circumpolar Current. The number in parentheses represents the trophic position estimated for each species based on $\delta^{15}\text{N}$ values

are related mainly with variation in physical (e.g. temperature), oceanographic (e.g. nutrient availability) and biological (e.g. primary producer composition) factors (Michener & Kaufman 2007 and references there in). This variation in baselines creates isotopic gradients along seascapes, and these have been well documented globally from inshore to offshore and benthic to pelagic habitats, as well as across latitudes (Rau et al. 1982, Goericke & Fry 1994, Quillfeldt et al. 2010). From the southwestern South Atlantic to Antarctic waters a negative isotopic trend in $\delta^{13}\text{C}$ and

$\delta^{15}\text{N}$ values was detected at the base of the food webs (e.g. POM; Lara et al. 2010) and propagated through the food chain, as was also revealed in several marine organisms (e.g. crustaceans, squids and fish) and top consumers (e.g. Quillfeldt et al. 2005, Cherel et al. 2008, Riccialdelli et al. 2010, Guerreiro et al. 2015). In fact, Cherel & Hobson (2007) and Phillips et al. (2009) found a correspondence between different water masses and $\delta^{13}\text{C}$ values, with abrupt changes at marine fronts, e.g. from the subantarctic to the Polar Front. The bone collagen isotope values from the beaked whale species studied in the present work reflects the general decrease in $\delta^{13}\text{C}$ values from nearshore areas of Tierra del Fuego to offshore and southern cold waters, such as the ACC and Antarctic regions. Thus, those species that forage at the same water masses show similar $\delta^{13}\text{C}$ values. $\delta^{15}\text{N}$ values are influenced by trophic position, and thus this complicates their use as habitat proxies (Cherel & Hobson 2007). However, we found important differences (up to 4.8‰) between northern and southern species—mainly attributable to spatial foraging areas—as a reflection of the variation in isotope composition at the base of food webs in organisms such as zooplankton, like krill, that exhibited raw $\delta^{15}\text{N}$ values ranging between ~2.6 and 7 ‰, these being lower in polar waters. As we expected, the TPs estimated for all beaked whale species were in general similar among species regardless of their foraging area, since they all feed on similar prey types. Therefore, differences in $\delta^{15}\text{N}$ values between beaked whales are driven by distinct isotopic nitrogen values at the base of food webs of different water masses, with higher $\delta^{15}\text{N}$ values characterizing waters adjacent to Tierra del Fuego and lower values characterizing polar waters.

In support of our findings, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from bone collagen of southern right whales (*Eubalena australis*) reported in this study target high-latitude offshore summer feeding grounds for this species in areas of the ACC (e.g. South Georgia and

Table 3. Stable isotope composition of possible prey species from subantarctic to Antarctic waters. Raw values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are means \pm SD; n = number of individuals analyzed or pooled information. Foraging area identified through stable isotope analysis: SW = subantarctic waters, ACC = Antarctic Circumpolar Current, PW = polar waters. Tissue analyzed: WB = whole body, M = muscle, B = bone collagen, BK = beak

Prey group/Species	Foraging area	n	$\delta^{13}\text{C}$ (‰)		$\delta^{15}\text{N}$ (‰)		C/N	Tissue	Source
			Mean	SD	Mean	SD			
Crustaceans									
<i>Euphausia lucens</i>	SW	7	-19.8	0.7	7.3	0.8		WB	Ciancio et al. (2008)
<i>Euphausia superba</i>	ACC	20	-26.3	1.5	3.5	0.6		WB	Schmidt et al. (2004)
	ACC	3	-22.6	1.0	4.0	0.3		WB	Schmidt et al. (2004)
	ACC	3	-22.7	2.3	5.3	0.4		WB	Schmidt et al. (2004)
	ACC	20	-22.3	3.1	4.3	1.0		WB	Stowasser et al. (2012)
	PW	33	-26.9	0.7	2.6	0.3	3.5	WB	Polito et al. (2013)
	PW	88	-26.4	1.0	3.5	0.7	3.4	WB	Polito et al. (2013)
	PW	59	-26.7	1.0	3.3	0.6	3.5	WB	Polito et al. (2013)
	PW	9	-25.1	0.9	4.2	0.4		WB	Schmidt et al. (2004)
	PW	9	-28.3	0.7	2.9	0.4		WB	Schmidt et al. (2004)
	PW	10	-26.5	0.4	3.2	0.4		WB	Polito & Goebel (2010)
	PW	20	-25.8	0.9	3.4	0.6	3.8	WB	Raya Rey et al. (2012)
	PW	12	-29.8	0.6	3.6	0.2	7.6	M	Dunton (2001)
Cephalopods									
<i>Illex argentinus</i>	SW	1	-16.6		14.9		3.3	M	Riccialdelli et al. (2013)
<i>Loligo gahi</i>	SW	10	-17.5	0.3	13.3	0.5	3.2	M	Riccialdelli et al. (2013)
<i>Taonius</i> sp. B (Voss)	SW	6	-21.4	0.9	11.5	0.6	3.3	BK	Alvito et al. (2015)
	SW	4	-21.9	1.5	9.9	1.0	3.3	BK	Alvito et al. (2015)
<i>Histioteuthis atlántica</i>	SW	10	-20.1	0.4	9.3	1.2	3.2	BK	Alvito et al. (2015)
<i>Histioteuthis macrohista</i>	SW	9	-19.6	0.3	10.2	0.8	3.2	BK	Alvito et al. (2015)
<i>Gonatus antarcticus</i>	ACC	6	-21.4	2.8	11.9	1.1	3.2	BK	Alvito et al. (2015)
	ACC	10	-21.7	1.7	10.8	0.7	3.1	BK	Alvito et al. (2015)
<i>Kondakovia longimana</i>	ACC	10	-21.9	1.5	8.0	0.8	3.2	BK	Alvito et al. (2015)
	ACC	10	-22.8	0.9	7.2	0.9	3.2	BK	Alvito et al. (2015)
<i>Batoteuthis skolops</i>	SW/PW	10	-23.8	0.4	9.0	0.6	3.3	BK	Alvito et al. (2015)
<i>Galiteuthis glacialis</i>	PW	10	-23.7	1.5	8.4	0.9	3.3	BK	Alvito et al. (2015)
	PW	6	-22.1	1.8	7.8	1.5	3.2	BK	Alvito et al. (2015)
Fish									
<i>Dissostichus eleginoides</i>	SW	1	-19.9		13.3		3.1	M	Present study
<i>Micromesistius australis</i>	SW	5	-15.8	0.8	13.1	0.7	2.8	B	Present study
<i>Macruronus magellanicus</i>	SW	9	-13.7	0.7	15.0	1.1	2.7	B	Riccialdelli et al. (2013)
<i>Merluccius australis</i>	SW	14	-14.0	0.7	16.8	1.0	2.8	B	Riccialdelli (2011), Zangrando et al. (2016)
<i>Gobionotothen gibberifrons</i>	ACC/PW	3	-24.9	0.9	10.1	0.7	4.5	M	Dunton (2001)
<i>Chaenocephalus aceratus</i>	ACC/PW	3	-24.9	0.1	11.0	0.6	4.3	M	Dunton (2001)
<i>Champscephalus gunnari</i>	ACC/PW	11	-23.5	0.6	9.6	0.2	3.2	M	Present study
<i>Chionodraco rastrospinosus</i>	PW	7	-23.8	0.5	9.2	0.1	3.2	M	Present study
<i>Lepidonotothen kempfi</i>	ACC	32	-23.1	1.0	11.6	0.3	3.3	M	Present study
<i>Notototheniops larseni</i>	ACC/PW	4	-22.0	2.6	12.4	0.0	3.3	M	Present study
<i>Pseudochaenichthys georgianus</i>	ACC/PW	22	-21.7	1.9	10.8	0.1	3.2	M	Present study

waters of the Polar Front; Rowntree et al. 2008, Valenzuela et al. 2009). Previous studies on *E. australis* have also measured low isotope values in skin samples (raw values near -23 and -6‰ in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively) from individuals in Argentina (Valenzuela et al. 2009) and on baleen plates (-26.5 and 4.0‰, in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively) from individuals stranded in South Africa (Best & Schell 1996) and in Argentina (-26.1‰ in $\delta^{13}\text{C}$; Rowntree et al. 2008) differentiating southern foraging areas for this

species. At another spatial extreme, bone collagen isotope values from northern and inshore species, such as *Cephalorhynchus commersonii* (Riccialdelli et al. 2013), targeted subantarctic feeding areas adjacent to Tierra del Fuego. Between these 2 extremes, an isotopic continuum among the beaked whales is clearly observed.

Species of beaked whales known to inhabit subantarctic temperate waters like *Tasmacetus shepherdi* and *Mesoplodon grayi* had high $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

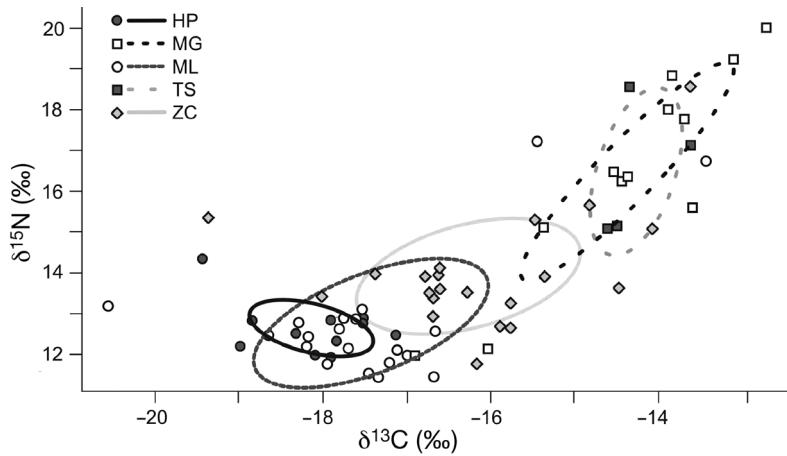


Fig. 3. Core isotopic niches of beaked whales. Lines enclose the standard ellipse area (SEAc) for each species estimated with SIBER (Jackson et al. 2011). HP = *Hyperoodon planifrons*; MG = *Mesoplodon grayi*; ML = *M. layardii*; TS = *Tasmacetus shepherdii*; ZC = *Ziphius cavirostris*

values. Almost nothing is known about the distribution of *T. shepherdii*, with only a few strandings (Bastida & Rodriguez 2009, Van Waerebeek et al. 2010) and few sightings confirmed at sea (Pitman et al. 2006). The isotope values of bone collagen of *T. shepherdii* analyzed in this work fell well within the general area that it was historically assumed to inhabit: deep and cold-temperate waters from 33° to 54° S of in the Southern Hemisphere (Pitman et al. 2006, Goodall et al. 2008, Van Waerebeek et al. 2010). *M. grayi* has a similar circumpolar distribution, which is found mostly between 30° to 55° S (Van Waerebeek et al. 2010).

Species that are known to inhabit Antarctic and subantarctic cold waters, including *Hyperoodon planifrons* and *Berardius arnuxii*, showed very low $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Both species are distributed throughout the Southern Ocean from the Antarctic pack-ice and up as far north as ~30° and ~40° S, respectively (Bastida & Rodriguez 2009, Van Waerebeek et al. 2010, Groom et al. 2014). Whilst *H. planifrons*

is considered to be the dominant beaked whale in polar waters (Santora & Brown 2010), there is little information on *B. arnuxii*, which probably inhabits small protected coastal inlets and bays (Friedlaender et al. 2010).

Between these 2 groups we found species that had intermediate $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (e.g. *Ziphius cavirostris*, *M. layardii* and *M. bowdoini*). Among them, *Z. cavirostris* is the most widely distributed (found from 0° to 64° S) and can be found mainly in warm-temperate oceanic waters; however, geographical overlap may occur with cold-southern species (MacLeod et al. 2003, Van Waerebeek et al. 2010). *M. bowdoini*, which is restricted to a narrow band north of the Antarctic Convergence

(Bastida & Rodriguez 2009), is only known from a few stranding records registered between 32° to 55° S. The specimen analyzed in this study corresponded to an adult male found stranded on the north-east coast of Tierra del Fuego (Bahía San Sebastián) in March 2003 (R. N. P. Goodall unpubl. data). Almost nothing is known about this species, but the only isotope value that we can provide here fell well in the general area that it is assumed to inhabit. *M. layardii* is also found throughout the southern oceans in temperate cold-waters from 33° to 60° S (Van Waerebeek et al. 2010). According to the isotope values reported in this study, we believe that the individuals analyzed may correspond to animals that inhabited the southern limit of their distribution. We hypothesized that this limit may correspond to the ACC, where species of both major groups—temperate vs. cold water species—overlap. It is known that the ACC is a complex and dynamic ocean region characterized by a series of frontal zones (Glorioso et al. 2005) that contain elevated concentrations of Antarctic krill (*E. superba*), myctophids

Table 4. Population metrics for beaked whale species. Nr = $\delta^{15}\text{N}$ range, Cr = $\delta^{13}\text{C}$ range, CD = distance to centroid, SDNND = standard deviation of mean nearest neighbor distance (Layman et al. 2007), SEAc = standard ellipse area corrected for small sample size (‰²), SEAc_B = Bayesian estimate of standard ellipse area (‰²), n = number of individuals used to calculate the metrics. Statistical comparison of isotopic niche widths is shown as the probability of one group to be smaller than other group resulting from the proportion of posterior draws of SEAc_B. Significant p-values (p < 0.05) are indicated in **bold**

Species	n	Cr	Nr	CD	SDNND	SEAc	SEAc _B	TS	MG	ZC	HP
<i>Tasmacetus shepherdii</i> (TS)	4	0.99	3.48	1.45	0.85	3.14	4.28				
<i>Mesoplodon grayi</i> (MG)	12	4.19	8.04	2.14	0.43	3.97	5.06	0.688			
<i>Ziphius cavirostris</i> (ZC)	23	5.75	6.80	1.48	0.73	5.44	5.32	0.253	0.414		
<i>Hyperoodon planifrons</i> (HP)	11	2.30	2.41	0.77	0.42	1.43	1.84	0.076	0.007	0.002	
<i>Mesoplodon layardii</i> (ML)	20	7.13	5.78	1.41	0.66	5.65	5.54	0.764	0.377	0.551	0.002

and squids and which provides habitat for a variety of top predators (Santora 2012), such as the beaked whale species analyzed in this study.

Finally, limited information exists for *M. hectori*. According to Rice (1998), this species inhabits mostly temperate waters; however, nothing suggests that it cannot occur in subantarctic and Antarctic waters (Van Waerebeek et al. 2010). Its geographic distribution was outlined from very few stranding records and should be considered tentative, due to the likelihood that these animals could appear stranded far from their normal distribution area. In addition, on many occasions they have been misidentified during sightings at sea due to the limited information on their external characteristics (Groom et al. 2014). The isotope values we provide here coincide with southern cold-water ocean regions, such as those inhabited by *B. arnuxii*; however, more analyses are needed in order to characterize its isotopic niche.

Trophic segregation: diet and trophic positions

Beaked whales are considered generalist predators that mainly feed in mesopelagic waters on squids and fish (MacLeod et al. 2003, MacLeod & D'Amico 2006), as their isotope values clearly showed in our study (Fig. 1). However, differences were found between genera and species. Most of the knowledge about the feeding preferences of beaked whales has come from stomach content analysis of stranded animals and from whaling operations. The isotope analysis performed in the present study complements previous information on their trophic habits and provides a longer-term record of dietary preferences free of many of the biases and limitations associated with the traditional methodology (reviewed in MacLeod et al. 2003, Pierce et al. 2004).

In general, our isotopic information was highly consistent with expected diet and TP estimations based on traditional methodology, such as stomach content analysis (Pauly et al. 1998, MacLeod et al. 2003). However, we found higher TPs in *H. planifrons* and *C. commersonii* compared to those calculated by Pauly et al. (1998). For the latter species, our results were consistent with Ciancio et al. (2008) and Riccialdelli et al. (2010), based on muscle and bone collagen isotope values, respectively. We also provided the first known TP estimations for *M. bowdoini*, *M. grayi*, *Phocoena dioptrica* and *Lagenorhynchus cruciger*.

Prey type is known to influence the stable isotope composition of a consumer. As an example, the ob-

served isotopic difference between southern beaked whales (e.g. *H. planifrons*) with *L. cruciger* and *P. dioptrica*, or with baleen whales, such as southern right whales (*E. australis*), are mostly due to diet. All these species are assumed to feed in the same ocean region, specifically ACC/PW (Riccialdelli et al. 2010, Dellabianca et al. 2012, Santora 2012). The southern right whale is known to consume mainly krill at higher latitudes (south of 50° S, i.e. around South Georgia Island), during its feeding season and large copepods at lower latitudes (north of 40° S) when they are not feeding on krill (Pauly et al. 1998, Rowntree et al. 2008, Valenzuela et al. 2009). These small crustaceans are characterized by low isotope values (from ~2.6 to 7‰ in $\delta^{15}\text{N}$) with respect to fish and squid from polar waters (e.g. Dunton 2001, Raya Rey et al. 2012, Guerreiro et al. 2015), which are the most important prey for beaked whales. The isotopic difference in prey species is reflected in the ^{13}C - and ^{15}N -enriched isotopic bone collagen values measured in beaked whales compared to lower trophic level consumers, such as *E. australis*. Also, southern beaked whales like *H. planifrons* had higher isotope values than *L. cruciger*. In this case, the isotopic differences observed mostly in $\delta^{15}\text{N}$ values (~2.5‰) may be due to the type of prey they can hunt since isotopic composition may vary depending on the size of the individual prey, which could also be available at different depths in the water column (e.g. Jennings et al. 2001, Cherel & Hobson 2005). The relatively small body size of *P. dioptrica* and *L. cruciger* in comparison to beaked whale species may constrain their diving capacities, as occurs in other marine mammal species (Noren et al. 2001). Thus, these 2 small cetaceans may be limited to epipelagic prey, such as myctophids, small squids and crustaceans (Goodall 1997).

Isotopic niche: trophic diversity and resource partitioning

As is stated in niche theory, most species do not occupy their full potential ('fundamental') niche due to interactions (e.g. competition) with other species, involving the concept of niche overlap that is usually measured in terms of resource utilization (Giller 1984). Interspecific competition may occur between species that overlap their niches if resource availability in the overlap zone cannot meet demand (limited resources); by contrast, if the resources are abundant, the species can coexist without competing with each other regardless of the overlap degree between them

(Giller 1984). However, sympatric similar species avoid competing by partitioning their niches, sometimes with subtle differences in food resources (Cloyed & Eason 2017). It has been proposed that isotopic niche area and the extent of overlap between isotopic areas can be used as a proxy to evaluate the trophic diversity and the degree of niche partitioning between species (Jackson et al. 2012). Thus, differences in isotopic niche areas between species may reflect differences in spatial foraging areas and/or feeding preferences.

M. layardii and *Z. cavirostris* exhibited the widest trophic diversity indicated by their largest SEAc. *Z. cavirostris* also showed high Cr and Nr values. These results can be explained in part by wider foraging areas (see 'Spatial segregation: foraging areas') and more diverse feeding preferences consistent with the lower TP estimated (3.9) in respect to other species. It is known that this species can feed in very deep waters, but also in pelagic waters, where they hunt crustaceans, fish and squids (Goodall & Galeazzi 1985, Blanco & Raga 2000, Adams et al. 2015), prey that are known to have remarkably different isotope values, as mentioned previously (see 'Trophic segregation: diet and trophic positions'). Possible seasonal movements between northern and southern areas within its geographic distribution (Sekiguchi et al. 1996, MacLeod et al. 2003) may explain a wide isotopic niche area and high Cr, Nr and CD values for *M. layardii*. However, in this species, 2 outliers with high $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values could be influencing the calculated metrics. We have no data on age estimation on these specimens, however, they were classified as juveniles based on their physical maturity (assessed by the state of epiphyseal fusion to the vertebra according to Goodall et al. 1988, 2008). An organism's niche may change in time and space as the biotic and abiotic environment varies. Marine predators can show a gradually changing niche since they can feed on different prey types at different marine areas and/or at different depth as they mature. Due to the low turnover rate, bone collagen from these 2 individuals can provide information on the foraging behavior from early years, such as lactation period. However, they do not show the common isotopic pattern of lactation with high $\delta^{15}\text{N}$ and low $\delta^{13}\text{C}$ values observed in other marine mammal species (e.g. Newsome et al. 2006, Orr et al. 2012, Riccialdelli et al. 2013). Also, as juveniles, they can be eating at a different depth and foraging area in respect to adults, which has a direct influence on collagen isotope values. More biological and ecological data is needed in order to evaluate different patterns of diet and/or habitat use within different ages.

T. shepherdii and *M. grayi* both showed a middle trophic diversity, whilst *H. planifrons* had a narrow trophic diversity. Due to its dentition, similar to other fish-eating odontocetes, *T. shepherdii* is assumed to feed more on fish rather than squids (MacLeod & D'Amico 2006). However, its diet is only known from 2 strandings, an individual stranded in north Patagonia (Argentina) with benthopelagic fish remains in its gut (e.g. *Merluccius hubbsi*) and from Tristan da Cunha Island (UK) with squids (MacLeod et al. 2003, Pitman et al. 2006). *M. grayi* seems to inhabit a wide range of water depths, with suggested nearshore movements in summer, and was also recorded south of the Polar Front (Van Waerebeek et al. 2010). Despite the fact that little is known about the diet of any of the 14 species of *Mesoplodon*, it seems that they prefer prey smaller (e.g. cephalopods <500 g) than those eaten by other genera of beaked whales (MacLeod et al. 2003). A small isotopic niche area for *H. planifrons* suggests a more specialized diet for this species and/or more restricted foraging areas in polar waters (see 'Spatial segregation: foraging areas').

We did not find any overlap within the *Mesoplodon* species analyzed, which could be the result of spatial segregation between them which may reduce any possible competition. Also, a possible trophic segregation may occur between sympatric *Mesoplodon* species and species of other genera, due to their different diet preferences, as was mentioned before. Indeed, *Z. cavirostris* seems to consume larger prey (>500 g) compared to *Mesoplodon* spp., which allows a sympatric distribution of the species from this genus. *M. layardii* showed an important isotopic niche overlap with *Z. cavirostris* and *H. planifrons*. This is probably generated by an overlap in their foraging grounds (see 'Spatial segregation: foraging areas'). Also, *H. planifrons* had an isotopic niche space that had a high overlap with that of *M. layardii*. However, the smaller isotopic niche area of *H. planifrons* may indicate a narrower range of resources exploited by this species. Regardless of the overlap, these species can co-exist in the same area since *M. layardii* exploits smaller food items than both *H. planifrons* and *Z. cavirostris* (MacLeod et al. 2003). In contrast, *H. planifrons* and *Z. cavirostris* appear to feed on similar types of prey (e.g. same size, MacLeod et al. 2003), but their isotopic niche spaces do not overlap at all. This result backs the idea that these species are geographically and probably temporally segregated in order to reduce any potential competition, as was suggested by MacLeod et al. (2003, 2004).

Our results confirm an important overlap in the isotopic niche between *T. shepherdii* and *M. grayi*, as

was also suggested by MacLeod et al. (2003) with conventional diet analysis, but with no other species studied in this work (e.g. *Ziphius* sp., *Hyperoodon* sp. and *Berardius* sp.). A widest foraging area can provide different types of prey for *M. grayi* and thus may explain a larger isotope niche space, a larger trophic diversity (CD), and also a higher range in carbon and nitrogen values compared to *T. shepherdii*. Unfortunately, we have so few data for *M. hectori* and *B. arnuxii* that we cannot reach any conclusion about niche partitioning between them and other beaked whales. However, both species showed the lowest $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in their bone collagen expected for polar waters predators (see 'Spatial segregation: foraging areas').

We acknowledge that, for some beaked whale species, our study relies on a sample size too small to provide robust conclusions about their isotopic niche widths and interspecific interactions. However, this situation will be progressively improved with the incorporation of further isotopic data as well as biological and ecological information gathered by other kinds of methodologies. Nonetheless, due to the extreme rarity of obtaining beaked whale samples and/or information about their trophic habits, this study provides useful and novel information about niche partitioning of these cetacean species. Also, in order to progress in the understanding of the isotopic ecology of any marine consumer, it is essential to continue in the resolution of the spatio-temporal isotopic baseline variation across ecosystems (e.g. POM, plankton). A general isotopic pattern is detected between inshore-offshore waters at the same latitude, between pelagic-benthic realms in the same area and across latitudes; however, the lack of data (e.g. isotopic and even biological data) can lead us to erroneous interpretations.

General conclusions

The species of beaked whales studied here include a number of poorly known species (Pitman et al. 2006). Our isotopic study, in combination with previous data, provides useful and novel ecological information about niche partitioning between these species. The following general conclusions can be drawn: (1) both distinctive foraging areas and prey types are influencing the isotopic niche of the cetaceans analyzed in this study; (2) the extent of overlap of the isotopic niches indicates the degree of similar resource utilization. Thus, a trophic (diet), spatial (foraging) and/or temporal difference can be expected for those species that have a substantial iso-

topic niche overlap (e.g. *M. grayi* and *T. shepherdii*); (3) spatial (foraging areas) segregation operates in species that share more similar diets, such as species of the same genus like *M. bowdoini*, *M. grayi*, *M. hectori* and *M. layardii*; (4) trophic (diet) differentiation can be expected between species that share foraging areas, such as *Z. cavirostris* and *M. grayi* and probably *M. bowdoini*, or between *Hyperoodon* and *M. layardii*; (5) a combination of spatial with temporal segregation can yield small isotopic niche overlap between species, such as between *Z. cavirostris* and *H. planifrons*. Beaked whales are considered important predators of oceanic marine ecosystems and are facing unclear consequences of many anthropogenic impacts (e.g. climate change, biological invasions, loud sounds from navy sonar and seismic exploration, discarded plastic debris and by-catch in gillnet and longline fisheries) (Secchi & Zarzur 1999, Cox et al. 2006). From a broader perspective, these impacts can alter fundamental ecological characteristics and ecosystem processes affecting the trophic interactions and the energy flows within ecosystems (Montoya et al. 2006, Sokolowski et al. 2014). To understand how species of beaked whales are impacted, we need to progress in the understanding of the ecological role they have in marine ecosystems.

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LITERATURE CITED

- ✦ Acha EM, Mianzan HW, Guerrero RA, Favero M, Bava J (2004) Marine fronts at the continental shelves of austral South America physical and ecological processes. *J Mar Syst* 44:83–105
- ✦ Adams J, Walker WA, Burton EJ, Harvey JT (2015) Stomach contents of a Cuvier's beaked whale (*Ziphius cavirostris*) stranded in Monterrey Bay, California. *Northwest Nat* 96:93–98

- Alvito PM, Rosa R, Phillips RA, Cherey Y and others (2015) Cephalopods in the diet of nonbreeding black-browed and grey-headed albatrosses from South Georgia. *Polar Biol* 38:631–641
- Ambrose SH (1990) Preparation and characterization of bone and tooth collagen for isotopic analysis. *J Archaeol Sci* 17:431–451
- Bastida R, Rodriguez D (2009) Marine mammals of Patagonia and Antarctica, 2nd edn. Vázquez Mazzini Editores, Buenos Aires
- Baum JK, Worm B (2009) Cascading top-down effects of changing oceanic predator abundances. *J Anim Ecol* 78: 699–714
- Bearhop S, Adams CE, Waldron S, Fuller RA, Macleod H (2004) Determining trophic niche width: a novel approach using stable isotope analysis. *J Anim Ecol* 73: 1007–1012
- Ben David M, Flaherty EA (2012) Theoretical and analytical advances in mammalian isotope ecology: an introduction. *J Mammal* 93:309–311
- Best PB, Schell DM (1996) Stable isotopes in southern right whale (*Eubalaena australis*) baleen as indicators of seasonal movements, feeding and growth. *Mar Biol* 124: 483–494
- Bisi TL, Dorneles PR, Lailson-Brito J, Lepoint G and others (2013) Trophic relationships and habitat preferences of delphinids from the southeastern Brazilian coast determined by carbon and nitrogen stable isotope composition. *PLOS ONE* 8:e82205
- Blanco C, Raga JA (2000) Cephalopod prey of two *Ziphius cavirostris* (Cetacea) stranded on the western Mediterranean coast. *J Mar Biol Assoc UK* 80:381–382
- Botta S, Hohn A, Macko SA, Secchi ER (2012) Isotopic variation in delphinids from the subtropical western South Atlantic. *J Mar Biol Assoc UK* 92:1689–1698
- Browning NE, Cockcroft VG, Worthy GAJ (2014) Resource partitioning among South African delphinids. *J Exp Mar Biol Ecol* 457:15–21
- Cabana G, Rasmussen JB (1996) Comparison of aquatic food chains using nitrogen isotopes. *Proc Natl Acad Sci USA* 93:10844–10847
- Cherey Y, Hobson KA (2005) Stable isotopes, beaks and predators: a new tool to study the trophic ecology of cephalopods, including giant and colossal squid. *Proc Biol Sci* 272:1601–1607
- Cherey Y, Hobson KA (2007) Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. *Mar Ecol Prog Ser* 329:281–287
- Cherey Y, Le Corre M, Jaquemet S, Ménard F, Richard P, Weimerskirch H (2008) Resource partitioning within a tropical seabird community: new information from stable isotopes. *Mar Ecol Prog Ser* 366:281–291
- Ciancio JE, Pascual MA, Botto F, Frere E, Iribarne O (2008) Trophic relationships of exotic anadromous salmonids in the southern Patagonian Shelf as inferred from stable isotopes. *Limnol Oceanogr* 53:788–798
- Cloyed CS, Eason PK (2017) Niche partitioning and the role of intra-specific niche variation in structuring a guild of generalist anurans. *R Soc Open Sci* 4:170060
- Coplen TB, Krouse HR, Bohle JK (1992) Reporting of nitrogen-isotope abundances. *Pure Appl Chem* 64:907e908
- Coplen TB, Brand WA, Gehre M, Gröning M, Meijer HAJ, Toman B, Verkouteren RM (2006) New guidelines for $\delta^{13}\text{C}$ measurements. *Anal Chem* 78:2439–2441
- Cox TM, Ragen TJ, Read AJ, Vos E and others (2006) Understanding the impacts of anthropogenic sound on beaked whales. *J Cetacean Res Manag* 7:177–187
- Cury P, Bakun A, Crawford RJM, Jarre A, Quiñones RA, Shannon LJ, Vergeye HM (2000) Small pelagics in upwelling systems: patterns of interaction and structural changes in 'wasp-waist' ecosystems. *ICES J Mar Sci* 57: 603–618
- Dellabianca N, Scioscia G, Schiavini A, Raya Rey A (2012) Occurrence of hourglass dolphin (*Lagenorhynchus cruciger*) and habitat characteristics along the Patagonian Shelf and the Atlantic Ocean sector of the Southern Ocean. *Polar Biol* 35:1921–1927
- DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. *Geochim Cosmochim Acta* 42:495–506
- DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. *Geochim Cosmochim Acta* 45:341–351
- Dunton K (2001) $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ measurements of Antarctic peninsula fauna: trophic relationships and assimilation of benthic seaweeds. *Am Zool* 41:41–99
- Francey RK, Allison CE, Etheridge DM, Trudinger CM and others (1999) A 1000 year record of $\delta^{13}\text{C}$ in atmospheric CO_2 . *Tellus B Chem Phys Meteorol* 51:170–193
- Friedlaender AS, Nowacek DJ, Johnston DW, Read AJ, Tyson RB, Peavey L (2010) Multiple sightings of large groups of Arnoux's beaked whales (*Berardius arnouxii*) in the Gerlache Strait, Antarctica. *Mar Mamm Sci* 26: 226–233
- Giller PS (1984) Community structure and the niche. Chapman & Hall, New York, NY
- Glorioso PD, Piola AR, Leben RR (2005) Mesoscale eddies in the subantarctic front – Southwest Atlantic. *Sci Mar* 69: 7–15
- Goericke R, Fry B (1994) Variations of marine plankton $\delta^{13}\text{C}$ with latitude, temperature, and dissolved CO_2 in the world ocean. *Global Biogeochem Cycles* 8:85–90
- Gonfiantini R (1978) Standards for stable isotope measurements in natural compounds. *Nature* 271:534–536
- Goodall RNP (1997) Review of sightings of the hourglass dolphin, *Lagenorhynchus cruciger*, in the South American sector of the Antarctic and Subantarctic. *Rep Int Whal Commn* 47:1001–1013
- Goodall RNP, Galeazzi AR (1985) A review of the food habits of the small cetaceans of the Antarctic and Sub-Antarctic. In: Siegfried WR, Condy PR, Laws RM (eds) Antarctic nutrient cycles and food webs, Springer-Verlag, Berlin, p 566–572
- Goodall RNP, Galeazzi AR, Lichter AA (1988) Exploitation of small cetaceans off Argentina 1979–1986. *Rep Int Whaling Commn* 38:407–410
- Goodall RNP, Benegas LG, Boy CC, Dellabianca N, Pimper L, Ricciardelli L (2008) Review of small cetaceans stranded or incidentally captured on the coast of Tierra del Fuego, Argentina, over 33 years. *Sci Comm Doc SC/60/SM21*. International Whaling Commission, Cambridge
- Graham BS, Koch PL, Newsome SD, McMahon KW, Aurioles D (2010) Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems. In: West J (ed) Isoscapes: understanding movement, pattern, and process on earth through isotope mapping. Springer, Berlin, p 299–318
- Groom C, Coughran DK, Smith HC (2014) Records of

- beaked whales (family Ziphiidae) in Western Australian waters. *Mar Biodivers Rec* 7:e50
- Guerreiro M, Phillips RA, Chérel Y, Ceia FR, Alvito P, Rosa R, Xavier JC (2015) Habitat and trophic ecology of Southern Ocean cephalopods from stable isotope analyses. *Mar Ecol Prog Ser* 530:119–134
- Hare PE, Fogel ML, Stafford TW Jr, Mitchell AD, Hoering TC (1991) The isotopic composition of carbon and nitrogen in individual amino acids isolated from modern and fossil proteins. *J Archaeol Sci* 18:277–292
- Hedges REM, Stevens RE, Koch PL (2005) Isotopes in bones and teeth. In: Leng MJ (ed) *Isotopes in palaeoenvironmental research*. Springer, Dordrecht, p 117–145
- Hobson KA, Welch HE (1992) Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. *Mar Ecol Prog Ser* 84:9–18
- Hobson KA, Chérel Y (2006) Isotopic reconstruction of marine food webs using cephalopod beaks: new insight from captive raised *Sepia officinalis*. *Can J Zool* 84:766–770
- Hoesinghaus DJ, Zeug SC (2008) Can stable isotope ratios provide for community-wide measures of trophic structure? *Comment. Ecology* 89:2353–2357
- Holt RD (2009) Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. *Proc Natl Acad Sci USA* 106:19659–19665
- Howland MR, Corr LT, Young SMM, Jones V and others (2003) Expression of the dietary isotope signal in the compound-specific $\delta^{13}\text{C}$ values of pig bone lipids and amino acids. *Int J Osteoarchaeol* 13:54–65
- Hutchinson GE (1957) Concluding remarks: Cold Spring Harbor symposium. *Quant Biol* 22:415–27
- Idermühle A, Stocker T, Joos F, Fisher H and others (1999) Holocene carbon-cycle dynamics based on CO_2 trapped in ice at Taylor Dome, Antarctica. *Nature* 398:121–126
- Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER—stable isotope Bayesian ellipses in R. *J Anim Ecol* 80:595–602
- Jackson MC, Donohue I, Jackson AL, Britton JR, Harper DM, Grey J (2012) Population-level metrics of trophic structure based on stable isotope and their application to invasion ecology. *PLOS ONE* 7:e31757
- Jennings S, Pinnegar JK, Polunin NVC, Boon TW (2001) Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. *J Anim Ecol* 70:934–944
- Koch PL (2007) Isotopic study of the biology of modern and fossil vertebrates. In: Michener R, Lajtha K (eds) *Stable isotopes in ecology and environmental science*, 2nd edn. Blackwell Publishing, Malden, MA, p 99–154
- Lara RJ, Alder V, Franzosi CA, Kattner G (2010) Characteristics of suspended particulate organic matter in the southwestern Atlantic: influence of temperature, nutrient and phytoplankton features on the stable isotope signature. *J Mar Syst* 79:199–209
- Layman CA, Arrington DA, Montaña CG, Post DM (2007) Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology* 88:42–48
- MacLeod CD, D'Amico A (2006) A review of beaked whale behavior and ecology in relation to assessing and mitigating impacts of anthropogenic noise. *J Cetacean Res Manag* 7:211–221
- MacLeod CD, Mitchell G (2006) Key areas for beaked whales worldwide. *J Cetacean Res Manag* 7:309–322
- MacLeod CD, Santos MB, Pierce GJ (2003) Review of data on diets of beaked whales: evidence of niche separation and geographic segregation. *J Mar Biol Assoc UK* 83:651–665
- MacLeod CD, Pierce GJ, Santos MB (2004) Geographic and temporal variations in strandings of beaked whales (Ziphiidae) on the coasts of the UK and the Republic of Ireland from 1800–2002. *J Cetacean Res Manag* 6:79–86
- MacLeod CD, Perrin WF, Pitman R, Barlow J and others (2006) Known and inferred distributions of beaked whale species (Cetacea: Ziphiidae). *J Cetacean Res Manag* 7:271–286
- Michener RH, Kaufman L (2007) Stable isotope ratios as tracers in marine food webs: an update. In: Michener R, Lajtha K (eds) *Stable isotopes in ecology and environmental science*, 2nd edn. Blackwell Publishing, Malden, MA, p 238–282
- Minagawa M, Wada E (1984) Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochim Cosmochim Acta* 48:1135–1140
- Montoya JM, Pimm SL, Sole RV (2006) Ecological networks and their fragility. *Nature* 442:259–264
- Newsome SD, Koch PL, Etnier MA, Aurioles-Gamboa D (2006) Using carbon and nitrogen isotope values to investigate maternal strategies in Northeast Pacific otariids. *Mar Mamm Sci* 22:556–572
- Newsome SD, Martinez del Río C, Bearhop S, Phillips DL (2007) A niche for isotopic ecology. *Front Ecol Environ* 5:429–436
- Newsome SD, Clementz MT, Koch PL (2010) Using stable isotope biogeochemistry to study marine mammal ecology. *Mar Mamm Sci* 26:509–572
- Noren SR, Williams TM, Pabst DA, McLellan WA, Dearolf JL (2001) The development of diving in marine endotherms: the skeletal muscles of dolphins, penguins, and seals for activity during submergence. *J Comp Physiol B* 171:127–134
- Orr AJ, Newsome SD, Laake JL, VanBlaricom GR, DeLong RL (2012) Ontogenetic dietary information of the California sea lion (*Zalophus californianus*) assessed using stable isotope analysis. *Mar Mamm Sci* 28:714–732
- Otley H (2012) The composition of the cetacean community in the Falkland (Malvinas) Islands, southwest South Atlantic Ocean. *Rev Biol Mar Oceanogr* 47:537–551
- Otley H, Smith J, Dalebout ML (2012) Beaked whale strandings on the Falkland Islands and South Georgia, South Atlantic Ocean, between 1866 and 2008. *J Mar Biol Assoc UK* 92:1851–1864
- Parnell AC, Inger R, Bearhop S, Jackson AL (2010) Source partitioning using stable isotopes: coping with too much variation. *PLOS ONE* 5:e9672
- Pauly D, Trites AW, Capuli E, Christensen V (1998) Diet composition and trophic levels of marine mammals. *J Mar Sci* 55:467–481
- Phillips DL (2012) Converting isotope values to diet composition: the use of mixing models. *J Mammal* 93:342–352
- Phillips RA, Behor S, Megill RAR, Dawson DA (2009) Stable isotopes reveal individual variation in migration strategies and habitat preferences in a suite of seabirds during the nonbreeding period. *Oecologia* 160:795–806
- Pianka ER (1974) Niche overlap and diffuse competition. *Proc Natl Acad Sci USA* 71:2141–2145
- Pierce GJ, Begoña Santos M, Learmonth JA, Mente E, Stowasser G (2004) Methods for dietary studies on marine mammals. In: Briand F (ed) *Investigating the roles of*

- cetaceans in marine ecosystems. CIESM Publisher, Venice, p 29–36
- ✦ Pitman R, Van Helden AI, Best PB, Pym A (2006) Shepherd's beaked whale (*Tasmacetus shepherdi*) information on appearance and biology based on strandings and at-sea observation. *Mar Mamm Sci* 22:744–755
- ✦ Polito MJ, Goebel ME (2010) Investigating the use of stable isotope analysis of milk to infer seasonal trends in the diets and foraging habitats of female Antarctic fur seals. *J Exp Mar Biol Ecol* 395:1–9
- ✦ Polito MJ, Reiss CS, Trivelpiece WZ, Patterson WP, Emslie SD (2013) Stable isotopes identify an ontogenetic niche expansion in Antarctic krill (*Euphausia superba*) from the South Shetland Islands, Antarctica. *Mar Biol* 160: 1311–1323
- ✦ Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83: 703–718
- ✦ Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montaña CG (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotopes analyses. *Oecologia* 152:179–189
- ✦ Pusineri C, Chancollon O, Ringelstein J, Ridoux V (2008) Feeding niche segregation among the Northeast Atlantic community of oceanic top predators. *Mar Ecol Prog Ser* 361:21–34
- ✦ Quillfeldt P, McGill RAR, Furness RW (2005) Diet and foraging areas of Southern Ocean seabirds and their prey inferred from stable isotopes: review and case study of Wilson's storm-petrel. *Mar Ecol Prog Ser* 295:295–304
- ✦ Quillfeldt P, Masello JF, McGill RAR, Adams M, Furness RW (2010) Moving polewards in winter: a recent change in the migratory strategy of a pelagic seabird? *Front Zool* 7: 15
- ✦ Quillfeldt P, Ekschmitt K, Brickle P, McGill RAR, Wolters V, Dehnhard N, Masello JF (2015) Variability of higher trophic level stable isotope data in space and time – a case study in a marine ecosystem. *Rapid Commun Mass Spectrom* 29:667–674
- R Development Core Team (2008). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- ✦ Rau GH, Sweeney RE, Kaplan IR (1982) Plankton ^{13}C : ^{12}C ratio changes with latitude: differences between northern and southern oceans. *Deep-Sea Res A* 29:1035–1039
- ✦ Raya Rey A, Polito M, Archuby D, Coria N (2012) Stable isotopes identify age- and sex-specific dietary partitioning and foraging habitat segregation in southern giant petrels breeding in Antarctica and southern Patagonia. *Mar Biol* 159:1317–1326
- Reisinger RR, de Bruyn PJN, Bester MN (2011) Predatory impact of killer whales on pinniped and penguin populations at the Subantarctic Prince Edward Islands: fact and fiction. *J Zool (Lond)* 285:1–10
- ✦ Renner M, Arimitsu ML, Piatt JF (2012) Structure of marine predator and prey communities along environmental gradients in a glaciated fjord. *Can J Fish Aquat Sci* 69: 2029–2045
- Riccaldelli L (2011) Ecología trófica de cetáceos subantárticos utilizando el análisis de isótopos estables. PhD thesis, Universidad Nacional de La Plata, Buenos Aires
- ✦ Riccaldelli L, Newsome SD, Fogel ML, Goodall RNP (2010) Isotopic assessment of prey and habitat preferences of a cetacean community in the southwestern South Atlantic Ocean. *Mar Ecol Prog Ser* 418:235–248
- ✦ Riccaldelli L, Newsome SD, Dellabianca NA, Bastida R, Fogel ML, Goodall RNP (2013) Ontogenetic diet shift in Commerson's dolphin (*Cephalorhynchus commersonii commersonii*) off Tierra del Fuego. *Polar Biol* 36:617–627
- Rice DW (1998) Marine mammals of the world: systematics and distribution. Spec Pub No. 4, The Society for Marine Mammalogy. Allen Press, Lawrence, KS
- Rowntree VJ, Valenzuela LO, Fraguas PF, Seger J (2008) Foraging behaviour of southern right whales (*Eubalaena australis*) inferred from variation of carbon stable isotope ratios in their baleen. *Sci Comm Doc SC/60/BRG23*. International Whaling Commission, Cambridge
- ✦ Ryan C, McHugh B, Trueman CN, Sabin R and others (2013) Stable isotope analysis of baleen reveals resource partitioning among sympatric rorquals and population structure in fin whales. *Mar Ecol Prog Ser* 479:251–261
- ✦ Santora JA (2012) Habitat use of hourglass dolphins near the South Shetland Islands, Antarctica. *Polar Biol* 35: 801–806
- ✦ Santora JA, Brown ET (2010) Spatial distribution patterns of southern bottlenose whales, *Hyperoodon planifrons*, near the South Shetland Islands, Antarctica. *Mar Mamm Sci* 26:960–968
- ✦ Schmidt K, McClelland JW, Mente E, Montoya JP, Atkinson A, Voss M (2004) Trophic-level interpretation based on $\delta^{15}\text{N}$ values: implications of tissue-specific fractionation and amino acid composition. *Mar Ecol Prog Ser* 266: 43–58
- Secchi ER, Zarzur S (1999) Plastic debris ingested by a Blainville's beaked whale, *Mesoplodon densirostris*, washed ashore in Brazil. *Aquat Mamm* 25:21–24
- ✦ Sekiguchi K, Klages NTW, Best PB (1996) The diet of strap-toothed whales (*Mesoplodon layardii*). *J Zool (Lond)* 239: 453–463
- ✦ Sokolowski A, Szczepariska A, Richard P, Kedra M, Wolowicz M, Weslawski JM (2014) Trophic structure of the macrobenthic community of Hornsund, Spitsbergen, based on the determination of stable carbon and nitrogen isotopic signatures. *Polar Biol* 37:1247–1260
- ✦ Stowasser G, Atkinson A, McGill RAR, Phillips RA, Collins MA, Pond DW (2012) Food web dynamics in the Scotia Sea in summer: a stable isotope study. *Deep Sea Res II* 59-60:208–221
- Valenzuela LO, Sironi M, Rowntree V, Seger J (2009) Isotopic and genetic evidence for culturally inherited site fidelity to feeding grounds in southern right whales (*Eubalaena australis*). *Mol Ecol* 18:782–791
- Van Waerebeek K, Leaper R, Baker AN, Papastavrou V and others (2010) Odontocetes of the Southern Ocean Sanctuary. *J Cetacean Res Manag* 11:315–346
- ✦ Whitehead H, MacLeaod CD, Rodhouse P (2003) Differences in niche breath among some teuthivorous mesopelagic marine mammals. *Mar Mamm Sci* 19:400–406
- Wiens JA, Stralberg D, Jongsomjit D, Howell CA, Snyder MA (2009) Niches, models, and climate change: assessing the assumptions and uncertainties. *PNAS* 106: 19729–19736
- Zangrando AF, Riccaldelli L, Kochi S, Nye JW, Tessone A (2016) Stable isotope evidence supports pelagic fishing by hunter-gatherers in southern South America during the Late Holocene. *J Archaeol Sci: Reports* 8:486–491